Soil attributes and microclimate are important drivers of initial deadwood decay in sub-alpine Norway spruce forests

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Soil attributes and microclimate are important drivers of initial deadwood decay in sub-alpine Norway spruce forests

Fravolini Giulia[a], Egli Markus[b*], Derungs Curdin[b], Cherubini Paolo[c], Ascher-Jenull Judith[d,e], Gómez-Brandón María[d], Bardelli Tommaso[d,e], Tognetti Roberto[a,g], Lombardi Fabio[f], Marchetti Marco[a]

[a]Department of Bioscience and Territory, University of Molise, Contrada Fonte Lappone snc, 86090 Pesche (IS), Italy, email: giulia.fravolini@email.unimol.it, tognetti@unimol.it, marchettimarco@unimol.it

[b]Department of Geography, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland, email: markus.egli@geo.uzh.ch

[c]WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstrasse 111, 8903 Birmensdorf ZH, Switzerland, email: paolo.cherubini@wsl.ch

[d]Institute of Microbiology, University of Innsbruck, Technikerstr. 25d, 6020 Innsbruck, Austria, email: judith.ascher@unifi.it, Maria.Gomez-Brandon@uibk.ac.at

[e]Department of Agrifood and Environmental Science, University of Florence, Piazzale delle Cascine 28, I-50144 Florence, Italy, email: tommaso.bardelli@unifi.it

[f]Department of AGRARIA, Mediterranean University of Reggio Calabria, Località Feo di Vito – 89122 Reggio Calabria (RC), Italy, email: fabio.lombardi@unirc.it

[g]The EFI Project Centre on Mountain Forests (MOUNTFOR), Edmund Mach Foundation, San Michele all'Adige, Italy.

*Corresponding author. Tel.: +41 44 635 51 14; fax: +41 44 6356848

E-mail address: markus.egli@geo.uzh.ch (M. Egli)

Abstract

Deadwood is known to significantly contribute to global terrestrial carbon stocks and carbon cycling, but its decay dynamics are still not thoroughly understood. Although the chemistry of deadwood has been studied as a function of decay stage in temperate to subalpine environments, it has generally not been related to time. We therefore studied the decay (mass of deadwood, cellulose and lignin) of equal-sized blocks of *Picea abies* wood in soil-mesocosms over two years in the Italian Alps. The 8 sites selected were along an altitudinal sequence, reflecting different climate zones. In addition, the effect of exposure (north- and south-facing slopes) was taken into account. The decay dynamics of the mass of deadwood, cellulose and lignin were related to soil parameters (pH, soil texture, moisture, temperature) and climatic data. The decay rate constants of *Picea abies* deadwood were low (on average between 0.039 and 0.040 y^{-1}) and of lignin close to zero (or not detectable), while cellulose reacted much faster with average decay rate constants between 0.110 and 0.117 y^{-1}. Our field experiments showed that local scale factors, such as soil parameters and topographic properties, influenced the decay process: higher soil moisture and clay content along with a lower pH seemed to accelerate wood decay. Interestingly, air temperature negatively correlated with decay rates or positively with the amount of wood components on south-facing sites. It exerted its influence rather on moisture availability, i.e. the lower the temperature the higher the moisture availability. Topographic features were also relevant with generally slower decay processes on south-facing sites than on north-facing sites owing to the drier conditions, the higher pH and the lower weathering state of the soils (less clay minerals). This study highlights the importance of a multifactorial consideration of edaphic parameters to unravel the complex dynamics of initial wood decay.

Keywords: deadwood decay, soil, cellulose, lignin, exposure, Alps

1. Introduction

Deadwood and coarse woody debris (CWD) are important components in the functioning of forest ecosystems and their structure, as they are relevant for biodiversity, trophic chains, natural regeneration in forests, nutrient cycles and overall carbon storage (Harmon et al., 1986; Jonsson and Kruys, 2001; Russell et al., 2015). CWD includes fallen trees, fallen branches, pieces of fragmented wood, stumps and standing dead trees (snags) (Zhou et al., 2007). The amount of deadwood varies with forest management. It may comprise up to 160 m^3/ha or 40% of the total biomass volume in natural spruce forests (Bobiec 2002; Ranius et al., 2003; Bobiec et al., 2005), but is typically less than 5 % in managed forest stands (MCPFE 2007). Since CWD is relevant for both maintaining biodiversity and understanding global C dynamics (Kueppers et al., 2004; Stokland et al., 2012), quantifying and determining its properties has recently received more attention.

The decay rate of deadwood is governed by several factors such as the ratio of bark to wood, the tree species, the log diameter (and the log's geometry in general; MacMillan, 1988; Van der Wal et al., 2007), the contact with the forest floor (Ganjegunte et al., 2004) and the soil type (van der Wal et al., 2007). The decrease in deadwood density over time is usually estimated using a negative exponential model (Naesset, 1999; Chen et al., 2005). The single negative exponential model, particularly for short-term studies, is the one most commonly used to determine and categorise the decomposition rate (e.g., Olson, 1963; Harmon et al., 1986; Laiho and Prescott, 2004). Tobin et al. (2007) showed, however, that the decay constants might vary slightly as a function of decay class. How the decay rate of deadwood is affected by climate is basic information for understanding the C-cycle and other nutrients. However, little data is available, apart from some studies in the North-Western Pacific in the U.S. and Canada (Harmon et al., 1986; Daniels et al., 1997; Campbell and Laroque, 2007), a few experimental and field studies (Naesset, 1999; Storaunet and Rolstad, 2002; Lombardi et al., 2008; Herrmann and Bauhus, 2012) on the decay rates of different tree species in European forest ecosystems and some rough estimates and models (Storaunet, 2004; Mäkinen et al., 2006). Russell et al. (2014) used a modelling approach to estimate the decay constants for 36 tree species common to eastern US forests and were able to show that the decay constants increased from 0.024 y^{-1} (with a mean annual temperature of < 2.8°) to 0.040 y^{-1} (≥ 13.7°C). Furthermore, decay rates have been found (Ferschet et al., 2012; Cornelissen et al., 2012) to differ in response to (micro)climate features (e.g., wood moisture), species (e.g., wood quality) and site conditions (e.g., faster decay rates under warmer conditions).

Mountainous ecosystems are particularly sensitive to changing environmental conditions (Mountain Research Initiative EDW Working Group, 2015). New or alternative techniques for assessing the decay rates of deadwood in European forests, particularly in cool mountain regions, are needed to i) obtain more data and ii) overcome difficulties with existing approaches.

The often-used chronosequence approach, however, may be criticised since it uses the so-called snap-shot sampling. This may lead to an underestimation of the decay constant *k* or decay rate in general and an overestimation of the age and the mean residence time of deadwood (Kruys et al., 2002). Furthermore, the dating of deadwood is difficult, particularly for the decay classes 4 and 5 (Petrillo et al., 2016) since these are the most advanced decay stages (Hunter, 1990). Alternatively, sites can be revisited and the decay of different deadwood components such as snags and CWD monitored (Russell and Weiskittel, 2012), but this may be skewed by episodic mortality events and uncontrolled conditions. An additional difficulty in determining CWD decay is the fall rate of snags. They can remain upright for several years and decay much more slowly than fallen dead trees (Yatskov et al., 2003). This makes it difficult to determine a clear age trend in decay. The fall rates of snags in Europe are largely unknown and comparisons between tree species are almost impossible, but more data is available from North America, see, e.g. Hilger et al. (2012) and Dixon (2015) for overviews.

As deadwood decomposes, its chemical structure and composition change. The type and rate of changes are wood specific and dependent on extrinsic factors, such as climate and others. With time, deadwood becomes incorporated into surface organic soil horizons, where it contributes to the chemical heterogeneity of the forest floor (Strukelj et al., 2013). To better assess deadwood decay processes, the analysis of carbon, nitrogen, phosphorous contents, as well as lignin and cellulose concentrations has been proposed (Bütler et al., 2007; Saunders et al., 2011). Deadwood chemistry has recently been studied as a function of decay stage in temperate to subalpine environments (Lombardi et al., 2008; Strukeli et al., 2013; Petrillo et al., 2015), but only exceptionally related to time (Petrillo et al., 2016). Such information, however, would be necessary to detect how the dynamics of deadwood change with site conditions and climate. Petrillo et al. (2016) showed that the decay of *Picea abies* in Alpine environments is very slow.

The following research questions were posed: 1) Can we confirm the very slow decay rates of *Picea abies* (L) Karst. as determined by Petrillo et al. (2016) in an Alpine setting (Trentino, Italy) by using a field-experimental approach with controlled conditions?; 2) How fast do the major wood-compounds (cellulose and lignin) in *Picea abies* decay in this cool and humid mountain environment?; 3) How do the decay rates relate to microclimatic conditions and soil parameters? — We hypothesised that Norway spruce wood decay would be very slow but that it might be enhanced under moister (atmosphere and soil) and warmer conditions. We furthermore assumed that cellulose should decay relatively fast and that probably only small changes would be detectable for lignin.

2. Study area

Sites in Trentino (Val di Rabbi and Val di Sole, northern Italy) in the European Alps (Fig. 1, Table 1) were chosen to represent a typical mountain climate. The sites were particularly suitable because a comprehensive database about their soils was available and that they belong to an already existing observation network (Egli et al., 2006). To assess the contribution of climate, the decay processes were studied at sites with different a) exposures (north- vs south-facing), and b) altitudes (toposequence). Eight sites were selected along two climosequences: one north-facing and one south-facing ranging from 1200 m a.s.l. up to 2000 m a.s.l. (with 4 sites, pairs on each, resulting in a total of 8 sites).

The climate of the slope area ranges from subalpine to alpine (above the timberline), the mean annual temperature from 8.2 °C at the valley floor (about 750 m a.s.l.) to about 0 °C at 2300 m a.s.l., and the mean annual precipitation from approximately 800 to 1300 mm (Sboarina and Cescatti, 2004). The geological parent material at all sites is paragneiss debris which is acidic. The soil units are Cambisols, Umbrisols and Podzols (WRB: IUSS working group, 2014). Forests are dominated by Norway spruce and at higher altitudes by European larch (Petrillo et al., 2016), with the timberline close to 2000 – 2200 m a.s.l.

3. Materials and Methods

3.1 Experimental set-up

At each site of the climosequence, a field experiment using soil mesocosms was set up as described in Maestrini et al. (2014). A soil mesocosm is an open soil monolith enabling field-experiments under semi-controlled conditions. Mesocosms (10.2 cm diam., 20 cm long PVC tubes) were inserted in the summer of 2012 into the natural soil one year prior to the addition of the wood blocks at a distance of >1 m from large trees and >0.5 m from the adjacent mesocosms, leaving at the surface a border of about 1 cm (Fig. 2). Since the size and geometry of deadwood can strongly influence the decay mechanisms (Van der Wal et al., 2007), wood blocks of the same *Picea abies* tree were prepared having a uniform size of 2 cm x 5 cm x 5 cm. These wood blocks were added to the soil mesocoms and directly placed on top of the soil with three replicate mesocosms for each time step installed on each of the 8 study sites. The wood blocks were, thus, in contact with the soil surface from the very beginning of the experiment. The deadwood blocks were sampled after 12 (t1), 25 (t2), 52 (t3) and 104 weeks (t4) (Fig. 2), resulting in a total of 96 samples (including the 3 replicates), with five wood blocks (for chemical analyses) kept as controls for t0 and 50 wood blocks for weight and density control (t0). The wood blocks were collected (with lab-gloves), placed in plastic bags, and transported in cool-boxes to the laboratory. They were then air-dried at room temperature, cut-milled to 4 mm (Retsch mill), aliquoted into sterile Falcon tubes (50 mL) and stored at 4°C until further processing.

The dry weight of the wood blocks that were used in the mesocosms was determined by standard methods (48 h in the oven at 105°C). The fresh weight and dry weight were determined to assess the density and water content of the wood blocks. The initial dry weight (at the start of the experiment) was obtained from the wood blocks at t0 (n = 50).

3.2 Cellulose and lignin extraction

For the wood cellulose extraction, the powdered samples were first weighed and 10mg placed in Teflon bags (Leavitt and Danzer, 1993). They were washed then in 5% NaOH solution, twice at 60°C, and again three times using a 7% $NaClO_2$ solution and 96% CH_3COOH at 60 °C to ensure the pH was between 4 and 5. This procedure extracts lignin from the samples. The bags were dried in the oven at 50 °C and the cellulose content determined as the difference between the initial weight and dried samples.

Both the total lignin and the so-called Klason lignin, which is insoluble in strong acid (Dence and Lin, 1992), were determined. The Klason lignin was obtained in a sequential extraction where first the water-soluble compounds were extracted (Dence and Lin, 1992). Ultrapure water (80 °C) was then added to 1 g of each sample and stirred 3 times for 15 min. After centrifuging for 10 min at 4500 rpm, the samples were dried in the oven at 80 °C, washed three times with 5 ml of ethanol and then centrifuged again for 10 min at 4500 rpm. The supernatant was discarded before adding ethanol again and filtering the sample. The filters were dried over night at 60 °C. Afterwards, 3 mL of a 72% sulphuric acid (H_2SO_4) solution were added to 300 mg of the filter cake. This was stirred with 84 mL of ultrapure water and put into the autoclave for 1 h at 120 °C. The resulting solution was then filtered into ceramic crucibles and the liquid evaporated at 110 °C, before weighing the lignin in the crucibles (Klason lignin). The acid-soluble lignin (ASL; Klason, 1893) in the filtrate was determined using a photometer (Cary 50 conc UV-Visible Spectrophotometer; 205 nm). The total lignin is the sum of the ASL + the Klason lignin; this lignin fraction includes also other recalcitrant compounds, such as tannins, cutin and suberin.

3.3 Determination of mass losses of deadwood, cellulose and lignin and related decay rates

The decay rate can be estimated by relating the time-since-death to the density loss or mass loss of deadwood during a given time period (Busse, 1994; Melin et al., 2009). The decay rate is commonly expressed through a decay constant *k*, which indicates the density loss or mass loss per year. This constant is derived from a decay model (Harmon et al., 1986), which can be most simply expressed by the equation in the single-negative-exponential model:

$$x_t = x_0\, e^{-kt} \qquad (1)$$

where x_t is the density or mass of deadwood at a given time (t), and x_0 is the initial mass (Jenny et al., 1949; Olson, 1963) or density. The mass is a more reliable parameter because density may underestimate deadwood decay rates. In this investigation, we used the mass of the wood blocks. Individual decay rates were determined on the basis of total mass losses of the wood blocks, cellulose and lignin. As previously mentioned, decay rate constants may slightly vary during the whole decay process. Herrmann and Prescott (2008) detected that the decay patterns of pine and spruce were similar with the highest *k* between 6 and 14 years. The information retrieved from a single decay rate constant may, thus, not fully reflect the whole decomposition process.

Due to the faster decomposition of cellulose, lignin is relatively enriched. Lignin, however, also decomposes with time. To unravel the decay behaviour of these compounds, a summation-exponential model can be applied (Means et al., 1985; Mackensen et al., 2003), with the general form:

$$x_t = x_1 e^{-k_1 t} + x_2 e^{-k_2 t} \ldots + x_n e^{-k_n t} \qquad (2)$$

where x_t is the mass (or density) of deadwood at a given time, and $x_{1\ldots n}$ are partitioned parameters. Subsequently, the half-life of the deadwood mass, cellulose or lignin could be calculated:

$$t_{1/2} = \frac{ln(1/2)}{-k} \qquad (3)$$

where $t_{1/2}$ is the half-life and k is the decay constant. In addition to equation 1, the decay rate constants of spruce deadwood were also estimated on the basis of the mass loss within the observation period using an exponential regression approach.

Freschet et al. (2012), however, question the use of the negative exponential (although it is very commonly used). Therefore, other regression functions to describe the mass loss of deadwood and its compounds as a function of time were applied and compared to the previously mentioned approaches. This included a linear, a polynomial (2nd order) and two sigmoid functions. The first sigmoid function (sigmoid function 1) is described by an exponential decay model (cf. Lichter, 1998):

$$f(t) = a + (b - a)e^{-kt} \quad (4)$$

where a represents an asymptote, b the initial quantity, and k the decay constant. The second (sigmoid function 2) is given by (Lichter, 1998):

$$f(t) = \frac{a}{(1 + e^{b(t-e)})} + d \quad (5)$$

where a = range of the wood property, t = time, b = slope coefficient, c = time (in years) of the maximal rate of change and d = asymptotic value (t = ∞).

3.4 Soil parameters

The soil temperature was measured close to the mesocosms between July 2013 and June 2014 at 3 h intervals with miniature temperature loggers, iButton® (Schmid et al., 2012), placed 10 cm below the soil surface. Soil pH (H_2O) was determined using a soil:solution ratio of 1:10. Particle size-distribution of the <2 mm fraction was determined as a weight percentage (USDA scale) using the sieve-and-pipette method with prior oxidation of organic matter by hypochlorite (NaClO) (Patruno et al., 1997). Soil clay mineralogical data were available from Egli et al. (2006, 2007).

3.5 Statistical analysis

The statistical analyses were performed using the software IBM SPSS Statistics 21 and R (3.2.3). For visualisation, the ggplot package was used. The data distribution of the mass of cellulose, lignin, deadwood and their corresponding decay constant was tested using the Shapiro Wilk normality-test. If the result of the normality test was positive, parametric comparison methods were then adopted through a t-test or an analysis of variance (ANOVA). Otherwise, two non-parametric comparison tests were applied, the Mann-Whitney (U-test) and the Kruskal-Wallis test. Bonferroni-corrections were considered. These tests were used to see if differences between north- and south-facing sites or along the altitudinal gradient exist with respect to the decay rates (mass losses) of deadwood, cellulose or lignin. To explain the data distribution of cellulose, lignin and deadwood (decay rates and amount), explanatory variables such as altitude, exposure (north vs. south), air temperature, precipitation, soil moisture, soil temperature, soil-pH and grain size were used. For several parameters, however, only one measurement or one series of measurements (altitude, exposure, air temperature, etc.) exist. Instead of a mixed linear modelling, we decided for a particular type of correlation analyses. To avoid autocorrelation, one replicate out of the 3 data points of each site (8) was chosen arbitrarily and correlated to the explanatory variables. By permutation, only one value per site was chosen. For each correlation 3^8 combinations (i.e. a total of 6561) were possible. In consequence, a high number of permutations and subsequent correlations could be calculated and the stability of the model tested. We performed 100 correlations for each dependent and explanatory variable and displayed the corresponding standard deviation of the correlation coefficients. The relationship between the explanatory variables and cellulose, lignin and deadwood are shown in cross-plots. This procedure does not allow the calculation of a significance level, but trends could be detected. In addition, a subdivision into south- and north-facing sites was done giving rise to 3^4 permutations.

4. Results

4.1 Decay rates and half-lives

Over the two-year study, the detectable changes in wood mass, cellulose and lignin (Figs. 3 – 5) were rather small. In several cases almost no time trend was detectable for lignin (Fig. 5) while the mass of deadwood and cellulose exhibited a continuous loss.

Several functions were tested to describe the time trends. The exponential, linear and sigmoid functions often yielded quite comparable results (Table 2). Although some authors criticise the exponential approach, it nonetheless seemed to describe the trends (Table 2, Fig. 6) — in general — slightly better than the other approaches. With respect to the comparability of our results with other publications, it makes even more sense to use this approach.

Accordingly, the decay constants of deadwood varied from almost zero to a maximum of 0.145 y^{-1} (Table 3). The average *k*-values for deadwood were in the range of 0.039 to 0.040 y^{-1}, depending on the calculation procedure and exposure (Table 3). The biochemical data of deadwood are given in Figures 4 and 5. The amount of cellulose and lignin is not displayed as a concentration value but as a mass, obtained by multiplying the concentration of cellulose and lignin with the deadwood mass (Figs. 4 and 5). We obtained the average value of 0.110 y^{-1} for the decay constant of cellulose using the single negative exponential model and 0.117 y^{-1} using the exponential regression approach (Table 3).

Using the average *k*-values, the half-life could be calculated for deadwood and cellulose. The deadwood half-life seemed to vary (as an average) between 17 years (single negative exponential model) and 22 years (regression approach; negative values not considered). In fact, negative *k*-values are not possible for decaying material, and can be attributed to measurement uncertainties. The half-life for cellulose was on average about 19 years using the negative exponential model and only 8 years using the exponential regression approach. However, along the altitudinal gradient it varied (as an average of the sites) between 2 and 74 years (Table 3). For lignin, the calculation of the *k*-value and, thus, the half-life was difficult or impossible since the decay rates fluctuated around zero (Table 3).

4.2 Effects of selected environmental parameters on deadwood decay

Climatic and pedogenic data are given in Tables 1 and 4. The climate varies from temperate to boreal (according to the classification from Köppen, 1918). The texture of the soils is sandy loam to loam. The comparison of the wood parameters (decay rate constants and amount) cellulose, lignin and deadwood is visualised in Figs. 7 and 8. All soils are acidic with generally more acidic conditions on the north-facing sites.

Due to the potential risk of autocorrelation, the replicate values of wood components were used by permutation and related to the explanatory variables exposure (north vs. south), air temperature, precipitation, soil moisture, soil temperature, soil-pH and grain size. For this correlation analysis not only the decay rates but also the amount of cellulose, lignin and deadwood at the end of the experiment were taken into account. The decay rate of cellulose not only correlated with climatic parameters, such as e.g. annual precipitation, but also with soil parameters, such as the clay content. The south-facing sites showed a good relation of the cellulose decay rate to MAP, MAAT, soil moisture, soil-pH and particularly to the clay content (Table 5). The higher the clay and soil water content, the faster is the decay of cellulose. Climate exerted its influence over the mean annual precipitation (the higher this parameter, the higher the decay rate of cellulose) and temperature. With temperature, a negative relationship, however, was found. The cooler the climate the faster is the decay rate of cellulose. This negative relationship seems to be surprising. A lower temperature strongly correlates with an increase in soil moisture. As a consequence, the temperature predominantly seemed to interfere over moisture (the lower the temperature the higher the soil moisture that positively influenced the decay rates). On the north-facing sites, however, no particular correlation between the wood parameters and explanatory variables could be found while conditions are completely overlaid by moisture availability due to the lower thermal conditions.

In addition, the decay rate constants of deadwood did not seem to be affected by any of the explanatory factors (Table 5). The lignin decay rate constant was not included in the statistical evaluations since during the observation time the values were around zero.

However, when considering the mass of deadwood, cellulose and lignin at the end of the field experiment (i.e., after 2 years), a correlation analysis was rendered possible for all of the wood components. This remaining mass could then be compared to environmental parameters. Using this approach, cellulose showed the same correlations as previously mentioned. At the south-facing sites particularly, a close relation between the amount of cellulose and the explanatory variables MAP, MAAT, soil moisture, soil-pH and the clay content exists. Noteworthy is again the good correlation with the clay content (Table 5). Quite a similar situation could be found for the mass of lignin and deadwood when related to the these environmental parameters. Whichever comparison is taken, it seemed that the clay content and the amount of precipitation were key variables for the decay of deadwood.

The Mann-Whitney test indicated that cellulose decayed significantly (p = 0.04; Table 6) faster at the north-facing sites, apart from the uppermost sites (N4 and S9). The cellulose half-life seemed to be higher on the south-facing sites to about 1800 m a.s.l., reaching in one case a value of as much as 118 years. Both the decay rate constant and the amount of cellulose differed significantly between north- and south-facing sites.

5. Discussion

5.1 Wood decomposition rates

The mesocosms approach showed that deadwood decays relatively slowly in the Alpine environment we investigated. Although the observation period of 2 years was rather short, the experimental approach, carried out under controlled conditions, enabled the derivation of rate constants for cellulose and deadwood and to recognise relationships between wood parameters and explanatory (environmental and soil) variables.

The measured decay rates for deadwood were rather similar to those reported by Petrillo et al. (2016) who determined the mean rates for spruce to be in the range of 0.018 to 0.022 y^{-1} using a chronosequence approach. The average rates determined in this study were between 0.039 and 0.040 y^{-1}, and were also in line with results reported by Herrmann et al. (2015) for Norway spruce in Central Europe. Decomposition rate constants of lying CWD of *P. abies* and *P. sylvestris* were 0.033 y^{-1} and 0.032 y^{-1}, respectively (Herrmann et al., 2015). One plausible explanation for the lower rates empirically determined by Petrillo et al. (2016) could be related to the time lag between the death of a standing tree and its contact with the soil (Kueppers et al., 2004; Zielonka, 2006; Lombardi et al., 2013; Petrillo et al., 2016). Standing dead trees can remain upright for several years and therefore decay much more slowly than fallen dead trees (Yatskov et al., 2003). Moreover, some parts of living trees may start to decompose before dying and therefore decay faster than non-decayed wood after death (Lombardi et al., 2008).

Decay rates are often derived from reductions in wood density through time, which when used to model biomass and carbon depletion are known to underestimate decay rate loss because they fail to account for volume reduction (changes in log shape) as decay progresses (Fraver et al., 2013). This also might explain why Petrillo's et al. (2016) decay rate constants were slightly lower than those in our and other studies, such as that of Rock et al. (2008).

The size of the deadwood also matters to a certain extent during the decay process (Tarasov and Birdsey, 2001). Usually, the smaller the size of deadwood the faster the decomposition rate. Based on a chronosequence approach, Tarasov and Birdsey (2001) determined quite similar decay rates with k = 0.059 y^{-1} using *Picea abies* (L.) karst wood pieces having a size of 5 – 20 cm in diameter. *Picea abies* bark (size < 20 cm) showed decay rates of 0.068 y^{-1} (Shorohova et al., 2008). Owing to the low k values, the deadwood of this tree species therefore constitutes a long-term carbon pool and a source of nutrients for biota in mountain forests. Furthermore, the k-values we obtained fit reasonably well with those of Russell et al. (2015). For environments where the mean annual temperature is < 8 °C, the decay rate constants are mostly < 0.06 y^{-1}, and may even be below 0.04 y^{-1} (Mackensen et al., 2003). The differences between the different experimental studies are probably also due to the uncertainty over the cause of death and the conditions of the decomposition.

Means et al. (1985) were able to derive *k* values for cellulose values of 0.0109 – 0.0117 y^{-1} for Douglas fir logs (in a cool to temperate climate). Petrillo et al. (2016) determined a decay rate constant of 0.032 y^{-1} for cellulose for spruce (*Picea abies*) and 0.014 y^{-1} for larch (*Larix decidua*). The average values of the cellulose decay rate constant in our experiment were in the range of 0.095 and 0.117 y^{-1}. Compared to Petrillo et al. (2016) these values are higher. In contrast to Means et al. (1985) or Petrillo et al. (2016), contact with the soil was given in our experiment from the outset. In addition, we used the wood mass to calculate rates that may give rise to higher *k* values.

No changes in the amount of lignin over the two-year observation period could be detected. This may be due to two reasons: i) No observed changes might be due to a lag period that passes before the decay of lignin truly begins. Such lag periods are usually observed for deadwood when the contact with soil is initially not given (Kueppers et al., 2004; Zielonka, 2006; Lombardi et al., 2013). In this investigation, this was not the case. Furthermore, the single-exponential model (Olson, 1963) does not always adequately describe the deadwood decomposition process (Harmon et al., 2000) due to a time lag required for decomposers to become established (Harmon et al. 2000; Hérault et al., 2010). In our investigation, this might probably be the case in those situations where the sigmoid functions better described the measured trend (Table 2, Fig. 6). ii) Lignin decomposes much slower than cellulose and the overall mass of deadwood. As such, the recorded changes over time (within these two years) were probably too small to be detected due to the insensitivity of the methods used. Petrillo et al. (2016) stated that the decay rate constant of lignin is a factor of about 5 – 10 lower than for cellulose (spruce, larch). Accordingly, the results are partially limited due to the rather short observation period (i.e., 2 years).

Nonetheless, our field experimental approach confirmed the very low decay rates of Norway spruce deadwood in Alpine environments, despite all of these potential ambiguities. All in all, lignin seems to decompose very slowly (and almost not detectable over a two-year observation period) whereas cellulose reacts rather fast and gives a well-discernible trend.

5.2 Relation of deadwood decay to soil and climatic parameters

Local scale factors do influence the decay dynamics, especially those factors that are related to the soil or the substrate and to the wood itself (Liu et al., 2013). Soil related parameters were only in very rare cases taken into account when measuring the decay rates of deadwood (e.g. Bütler et al., 2007; van der Wal et al., 2007; Risch et al., 2013). The decay dynamics at the local scale of our investigation area were influenced not only by air temperature and annual precipitation, but also by soil acidity (pH), soil moisture and the grain size (i.e., clay content) (Table 5). However, not all of the wood components reacted similarly. In this sense, cellulose decays much faster than lignin or the bulk deadwood. Consequently, the relations of cellulose with environmental and soil parameters could be better tested and were in some cases particularly good. Owing to the slow and almost not detectable decay, lignin is important in stocking organic carbon in the long-term and thus for ensuring a stable background source of organic carbon for the forest soil. This might affect processes of deadwood decay and the formation of humic substances since decomposing organisms react differently to wood cellulose and lignin (Stokland et al., 2012; Lombardi et al., 2013). Cellulose is easily decomposed by (micro)organisms, particularly in coniferous trees with a relatively simple wood structure (Lambert et al., 1980; Laiho and Prescott, 2004). Compounds such as tannins and lignin may, however, restrict microbial colonisation and thus slow down wood decomposition (Baldock et al., 1997). Conifers are generally rather resistant to decay and tend to decompose more uniformly than broadleaves.

The mass of cellulose, lignin and deadwood (at the end of the experiment) and the cellulose decay rates correlated well with the clay content of the soils (Figs. 7 and 8; Table 5). Particularly at the south-facing sites, a close relationship of these parameters with explanatory variables indicating moisture (soil moisture, annual precipitation), temperature (mean annual air temperature) and soil pH was evident. As a consequence, soil parameters are not negligible when considering wood decay. Important explanatory variables are consequently the clay content, pH and soil moisture. These parameters are principally related to weathering processes and water availability. The clay content of the soils correlated well with soil-pH ($R = 0.91$, $p < 0.01$; Bonferroni corrections considered). Smectitic compounds (i.e. smectite + interstratified smectite-mica; Table 7), as an important part of the clays, positively correlated with soil moisture ($R = 0.78$, $p < 0.05$) and negatively with pH ($R = -0.81$, $p < 0.01$). The higher the smectite content the higher the moisture content and the lower the pH. Clays have the ability to better retain water and consequently improve water availability that is necessary for decay. Clay minerals are formed in these environments by weathering processes (transformation of primary minerals) that are more intense in cooler environments (Egli et al., 2006, 2010) having a lower pH. In addition, more expanding minerals (smectites) were measured on the cooler north-facing sites (particularly below 2000 m a.sl.) at the same study sites in previous investigations (Egli et al., 2006, 2007; Table 7). Smectites have the possibility to store water in their interlayers and to collapse after drying. The hydroxy interlayering of clay minerals, which prevents them from expansion, was more evident at south-facing sites (Table 7; Egli et al., 2007). As a consequence, north-facing sites have a greater potential to retain water.

A more intense weathering is often related to more acidic conditions. The more acidic, moister and cooler conditions gave rise to a more expressed weathering at the moister north facing sites. More specifically, at the north-facing sites N1 – N3 the clay content (depth 0 – 15 cm) was significantly higher (18 ± 2%) compared to the south-facing sites S6 – S8 (having 14 ± 0.9%). Furthermore, fungi, the principal decomposers of deadwood (Jacobs and Work, 2012; Stokland et al., 2012; Forrester et al., 2015; Hoppe et al., 2015a, b; van der Wal et al., 2015) prefer more acidic conditions that give rise to an enhanced wood decay. A nutrient-poor, strongly weathered substrate and low pH seems to increase stem rot. According to Heinemann et al. (2015), the frequency of stem rot increased significantly in soils with low pH and cation concentrations in topsoil. Soil acidity is known as a dominant factor affecting the soil microbial community structure (Ascher et al., 2012). The saproxylic food web, and especially the role of fungi, known to act as principal deadwood decomposers/digesters (brown rot-, soft rot-, white rot-) (Jacobs and Work, 2012; Stokland et al., 2012; Forrester et al., 2015; van der Wal et al., 2015), cannot be neglected when addressing the decay/decomposition-dynamics of deadwood. The composition of wood-inhabiting fungal communities is predominantly related to the physico-chemical properties of the deadwood substrate (Hoppe et al., 2015b). These properties seemed to also be governed by extrinsic environmental properties as previously mentioned.

Neither deadwood nor any of the wood components showed a strong relationship to soil temperature in our study, despite the fact that Risch et al. (2013) suggested that soil temperature was the main variable to explain the differences in the decay rates of aspen and pine. Herrmann and Bauhus (2012) observed that about 60% of the variation in the CO_2 flux of CWD of *P. abies* was explained by climatic variables (wood moisture and wood temperature) in a lab incubation experiment, whereas more than 90% of CWD respiration of individual *P. abies* logs was explained by temperature in a one-year field experiment. This comparison with other data shows again that moisture availability seems to be a stronger driver for decomposition than temperature alone.

5.3 Effect of exposure

North-facing sites are normally cooler than comparable south-facing sites, but unexpectedly decay rates on north-facing sites seemed to be higher up to an elevation of about 1800 m a.s.l., again most likely due to the different moisture availability. The soil moisture content was significantly lower on the south-facing sites (24.8%±10.6) than on the north-facing sites (38.9%±13.5), but evapotranspiration is higher. The soil conditions are thus drier on south-facing sites, even though annual precipitation is the same as on north-facing sites. Wood degradation is subsequently slow.

Shorohova and Kapitsa (2014) found that CWD decomposition was faster on sites with a moderate level of moisture than on dry sites, but CWD decay on wet sites is slow in boreal forests. The decay rate constant of 0.032 y^{-1} for Norway spruce (Shorohova and Kapitsa, 2014) is very similar to our study. The high variability of decomposition rates relates to water availability, local topography, soil composition and incoming radiation. Soil moisture controls nutrient availability and oxygen diffusion required for microbial decomposition (Skopp et al., 1990). Although climatic conditions have a strong impact on the wood decomposer community (Hoppe et al., 2015a,b), Norway spruce is relatively resistant to decay confirming the decay-rates to be tree-species specific.

6. Conclusions

From our measurements of decay rates under controlled conditions using a field-experimental approach we found:

- The decay rates of *Picea abies* deadwood in Alpine environments seem to be low. Although we used an experimental approach over a rather short time period with relatively small wood blocks, the detected decay rates could be compared moderately well to average values observed for the same species at other sites in Europe.
- Lignin decay rates were difficult to determine and fluctuated (over the observation period) around zero. In contrast, cellulose responded much faster and clear trends could be found.
- Local scale factors, such as soil parameters and topographic properties, are important and distinctly influence the decay dynamics of deadwood and its components. A higher soil moisture and clay content along with a lower pH – favourable conditions especially for fungal deadwood decomposers – accelerate the decay process. Temperature, interestingly, exerts rather an influence on the decay rates over moisture availability. The cooler the environment, the higher the moisture availability and the higher the decay rates. In contrast to other findings, our observations suggest that a lower temperature positively influenced the decay rates of cellulose.

- In Alpine areas, topographic exposure (south- vs north-facing sites) also affects decay processes, which are slower on south-facing sites below 1800 m a.s.l. owing to the drier conditions.

Although our study was conducted in one specific area of the Alps, the findings can be extrapolated to similar regions. Our results highlight the importance of the multiple edaphic and topographic factors that control deadwood decay processes in mountain forest ecosystems in conjunction with climate. Controlled settings allowed for a better discrimination of the processes involved. Longer-term measurements would be advisable to see if the low decomposition rates, particularly of lignin were due to a lag period. Further analyses of deadwood dynamics, including the input and decomposition of deadwood, are needed to better understand and model mountain forests, and predict their development after disturbances.

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References

Ascher, J., Sartori, G., Graefe, U., Thornton, B., Ceccherini, M.T., Pietramellara, G., Egli M., 2012. Are humus forms, mesofauna and microflora in subalpine forest soils sensitive to thermal conditions? Biol. Fert. Soils 48, 709-725.

Baldock, J.A., Oades, J.M., Nelson, P.N., Skene, T.M., Golchin, A., Clarke, P., 1997. Assessing the extent of decomposition of natural organic materials using solid-state ^{13}C NMR spectroscopy. Austr. J. Soil Res. 35, 1061-1083.

Bobiec, A., 2002. Living stands and deadwood in the Bialowieza forest: Suggestions for restoration management. For. Ecol. Manag. 165, 125–140.

Bobiec, A., Gutowski, J.M., Zub, K., Pawlaczyk, P., Laudenslayer, W.F., 2005. The afterlife of a tree. WWF Poland, Warszawa – Hajnówka.

Busse, M.D., 1994. Downed bole-wood decomposition in lodgepole pine forests of central Oregon. Soil Science Society of America J. 58, 221–227.

Bütler, R., Patty, L., Le Bayon, R.C., Guenat, C., Schlaepfe, R., 2007. Log decay of *Picea abies* in the Swiss Jura Mountains of Central Europe. For. Ecol. Manag. 242, 791–799.

Campbell, L.J., Laroque, C.P., 2007. Decay progression and classification in two old-growth forests in Atlantic Canada. For. Ecol. Manag. 238, 293-301.

Chen, X.Y., Wei, X.H., Scherer, R., 2005. Influence of wildfire and harvest on biomass, carbon pool, and decomposition of large woody debris in forested streams of southern interior British Columbia. For. Ecol. Manag. 208, 101–114.

Cornelissen, J.H., Sass-Klaassen, U., Poorter, L., van Geffen, K., van Logtestijn, R.S., van Hal, J., Goudzwaard, L., Sterck, F.J., Klaassen, R.K., Freschet, G.T., van der Wal, A., Eshuis, H., Zuo, J., de Boer, W., Lamers, T., Weemstra, M., Cretin, V., Martin, R., Ouden, Jd., Berg, M.P., Aerts, R., Mohren, G.M., Hefting, M.M., 2012. Controls on coarse wood decay in temperate tree species: birth of the LOGLIFE experiment. Ambio 41 Suppl. 3, 231-245.

Daniels, L.D., Dobry, J., Klinka, K., Feller, M.C., 1997. Determining year of death of logs and snags of Thujaplicata in south-western coastal British Columbia. Can. J. For. Res. 27, 1132–1141.

Dence, C.W., Lin, S.Y., 1992. Introduction. In: Lin, S.Y., Dence, C.W. (eds), Methods in lignin chemistry. Springer, Heidelberg, pp. 1–19.

Dixon, G.E., 2015. Essentials FVS: A User's Guide to the Forest Vegetation Simulator. United

States Department of Agriculture, US Forest Service, Fort Collins CO.

Egli, M., Mirabella, A., Sartori, G., Zanelli, R., Bischof, S., 2006. Effect of north and south exposure on weathering rates and clay mineral formation in Alpine soils. Catena 67, 155–174.

Egli, M., Mirabella, A., Sartori, G., Giaccai, D., Zanelli, R., Plötze, M., 2007. Effect of slope aspect on transformation of clay minerals in Alpine soils. Clay Minerals 42, 373-398.

Egli, M., Sartori, G., Mirabella, A., 2010. The effects of exposure and climate on the weathering of late Pleistocene and Holocene Alpine soils. Geomorphology 114, 466-482.

Forrester, J.A., Mladenoff, D.J., D'Amato, A.W., Fraver, S., Lindner, D.L., Brazee, N.J., Clayton, M.K., Gower, S.T., 2015. Temporal trends and sources of variation in carbon flux from coarse woody debris in experimental forest canopy openings. Oecologia 179, 889-900.

Fraver, S., Milo, A.M., Bradford, J.B., D'Amato, A.W.D., Kenefic, L., Palik, B.J., Woodall, C.W., Brissette, J., 2013. Woody debris volume depletion through decay: Implications for biomass and carbon accounting. Ecosystems 16, 1262-1272.

Freschet, G.T., Weedon, J.T., Aerts, R., van Hal, J.R., Cornelissen, J.H.C., 2012. Interspecific differences in wood decay rates: insights from a new short-term method to study long-term wood decomposition. J. Ecol. 100, 161-70.

Ganjegunte, G.K., Condron, L.M., Clinton, P.W., Davis, M.R., Mahieu, N., 2004. Decomposition and nutrient release from radiata pine (*Pinus radiata*) coarse woody debris. For. Ecol. Manag. 187, 197–211.

Harmon, M.E., Krankina, O.N., Sexton, J., 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. Can. J. For. Res. 30, 76-84.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D, Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133-302.

Heineman, K. D., Russo, S. E., Baillie, I. C., Mamit, J. D., Chai, P. P. -K., Chai, L., Hindley, E. W., Lau, B. -T., Tan, S., Ashton, P. S., 2015. Evaluation of stem rot in 339 Bornean tree species: implications of size, taxonomy, and soil-related variation for aboveground biomass estimates. Biogeosciences 12, 5735-5751.

Hérault, B., Beauchêne, J., Muller, F., Wagner, F., Baraloto, C., Blanc, L., Martin, J.-M., 2010. Modeling decay rates of dead wood in a neotropical forest. Oecologia 164, 243-251.

Herrmann, S., Prescott, C. E., 2008. Mass loss and nutrient dynamics of coarse woody debris in three Rocky Mountain coniferous forests: 21 years results. Can. J. For. Res. 38, 125-132.

Herrmann, S., Bauhus, J., 2012. Effects of moisture, temperature and decomposition stage on respirational carbon loss from coarse woody debris (CWD) of important European tree species. Scand. J. For. Res. 28, 346–357.

Herrmann, S., Kahl, T., Bauhus, J., 2015. Decomposition dynamics of coarse woody debris of three important central European tree species. For. Ecosyst. 2:27, DOI 10.1186/s40663-015-0052-5.

Hilger, A.B., Shaw, C.H., Metsaranta, J.M., Kurz, W.A., 2012. Estimation of snag carbon transfer rates by ecozone and lead species for forests in Canada. Ecol. Appl. 22, 2078–2090.

Hoppe, B., Purahong, W., Wubet, T. , Kahl, T., Bauhus, J., Arnstadt, T., Hofrichter, M., Buscot, F., Krüger, D., 2015a. Linking molecular deadwood-inhabiting fungal diversity and community dynamics to ecosystem functions and processes in Central European forests. Fungal Diversity DOI 10.1007/s13225-015-0341-x.

Hoppe, B., Krüger, D., Kahl, T., Arnstadt, T., Buscot, F., Bauhus, F., Wubet, T., 2015b. A pyrosequencing insight into sprawling bacterial diversity and community dynamics in decaying deadwood logs of *Fagus sylvatica* and *Picea abies*. Sci Rep. 5, 9456, doi:10.1038/srep09456.

Hunter, M.L., 1990. Wildlife, forests and forestry: principles of managing forests for biological diversity. Prentice Hall, Englewood Cliffs (NJ), USA.

IUSS Working Group WRB, 2014. International soil classification system for naming soils and creating legends for soil maps. World Reference Base for Soil Resources 2014 World Soil Resources Reports 106. FAO, Rome

Jacobs, J.M., Work, T.T., 2012. Linking deadwood-associated beetles and fungi with wood decomposition rates in managed spruce forests. Can. J. For. Res. 42, 1477-1490.

Jenny, H., Gessel, S.P., Bingham, F.T., 1949. Comparative study of decomposition of organic matter in temperate and tropical regions. Soil Sci. 68, 419–432.

Jonsson, B.G., Kruys, N., 2001. Ecology of Woody Debris in Boreal Forests. Ecol. Bull. 49, 279-281.

Köppen, W., 1918. Klassification der Klimate nach Temperatur, Niederschlag and Jahreslauf. IPetermanns Geog. Mitt. 64, 193–203 and 243–248.

Kruys, N., Jonsson, B.G., Ståhl, G., 2002. A stage-based matrix model for decay-class dynamics of woody debris. Ecol. Applic. 12, 773-781.

Kueppers, L.M., Sourthon, J., Baer, P., Harte, J., 2004. Dead wood biomass and turnover time, measured by radiocarbon, along a subalpine elevation gradient. Oecologia 141, 641–651.

Laiho, R., Prescott, C.E., 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Can. J. For. Res. 34, 763-777.

Lambert, R.L., Lang, G.E., Reiners, W.A., 1980. Loss of Mass and Chemical Change in Decaying Boles of a Subalpine Balsam Fir Forest. Ecol. 61, 1460-1473.

Leavitt, S.W., Danzer, S.R., 1993. Method for Batch Processing Small Wood Samples to Holocellulose for Stable-Carbon Isotope Analysis. Anal. Chem. 65, 87-89.

Lichter, J., 1998. Rates of weathering and chemical depletion in soils across a chronosequence of Lake Michigan sand dunes. Geoderma 85, 255-282.

Liu, W., Schaefer, D., Liu, X., 2013. What controls the variability of wood-decay rates? For. Ecol. Manag. 310, 623-631.

Lombardi, F., Cherubini, P., Lasserre, B., Tognetti, R., Marchetti, M., 2008. Tree rings used to assess time since death of deadwood of different decay classes in beech and silver fir forests in the central Apennines (Molise, Italy). Can. J. For. Res. 38, 821-833.

Lombardi, F., Cherubini, P., Tognetti, R., Cocozza, C., Lasserre, B., Marchetti, M., 2013. Investigating biochemical processes to assess deadwood decay of beech and silver fir in Mediterranean mountain forests. Ann. For. Sci, 70, 101–111.

Mackensen, J., Bauhus, J., Webber, E., 2003. Decomposition rates of coarse woody debris – A review with particular emphasis on Australian tree species. Aust. J. Bot. 51, 27–37.

MacMillan, P.C., 1988. Decomposition of coarse woody debris in old-growth Indiana forest. Can. J. For. Res. 18, 1353–1362.

Maestrini, B., Abiven, S., Singh, N., Bird, J.A., Torn, M.S., Schmidt, M.W.I., 2014. Carbon losses from pyrolysed and original wood in a forest soil under natural and increased N deposition. Biogeosciences 11, 5199-5213.

Mäkinen, H., Hynynen, J., Siitonen, J., Sievänen, R., 2006. Predicting the decomposition of scots pine, Norway spruce, and birch stems in Finland. Ecol. Appl. 16, 1865-1879.

MCPFE (Ministerial Conferences on the Protection of Forests in Europe) 2007. State of Europe's Forests 2007. The MCPFE Report on Sustainable Forest Management in Europe. MCPFE Liaison Unit Warsaw, UNECE and FAO.

Means, J. E., Cromack, K., and MacMillan, P. C., 1985. Comparison of decomposition models using wood density of Douglas-fir logs. Can. J. Forest R., 15, 1092-1098.

Melin, Y., Petersson, H., Nordfjell, T., 2009. Decomposition of stump and root systems of Norway spruce in Sweden – A modelling approach. For. Ecol. Manag. 257, 1445-1451.

Mountain Research Initiative EDW Working Group, 2012. Elevation-dependent warming in mountain regions of the world. Nat. Clim. Change 5, 424-430.

Naesset, E., 1999. Decomposition rate constants of Picea abies logs in southeastern Norway. Can. J. For. Res. 29, 372–381.

Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44, 322–331.

Patruno, A., Cavazza, L., Castriganò, A., 1997. Metodi di analisi fisica del suole, Parte III, 1. Ministero per le Politiche Agricole Osservatorio Nazionale Pedologico e per la Qualità del Suolo, in collaborazione con International Society of Soil Science, ISO/DIS 11277.

Petrillo, M., Cherubini, P., Sartori, G., Abiven, S., Ascher, J., Bertoldi, D., Barbero, A., Larcher, R., Egli, M., 2015. Biochemical characteristics of decomposing deadwood in an Alpine forest and their relation to climate. iForest 9, 154-164.

Petrillo, M., Cherubini, P., Fravolini, G., Marchetti, M., Ascher, J., Schärer, M., Synal, H.-A., Bertoldi, D., Camin, F., Larcher, R., Egli, M., 2016. Time since death and decay rate constants of Norway spruce and European larch deadwood in subalpine forests determined using dendrochronology and radiocarbon dating. Biogeochem. 13, 1537-1552.

Ranius, T., Kindvall, O., Kruys, N., Jonsson, B.G., 2003. Modeling dead wood in Norway spruce stands subject to different management regimes. For. Ecol. Manag. 182, 13–29.

Risch, A.C., Jurgensen, M.F., Page-Dumroese, D., Schütz, M., 2013. Initial turnover rates of two standard wood substrates following land-use change in subalpine ecosystems in the Swiss Alps. Can. J. For. Res. 43, 901-910.

Rock, J., Badeck, F., Harmon, M.E., 2008. Estimating decomposition rate constants for European tree species from literature sources. Eur. J. For. Res. 127, 301–313.

Russell, M.B., Fraver, S.F., Aakala, T., Gove, J.H., Woodall, C.W., D’Amato, A.W., Ducey, M.J., 2015. Quantifying carbon stores and decomposition in dead wood: A review. For. Ecol. Manag. 350, 107-128.

Russell, M.B., Woodall, C.W., Fraver, S., D’Amato, A.W., Domke, G.M., Skog, K.E., 2014. Residence times and decay rates of downed woody debris biomass/carbon in Eastern US forests. Ecosystems 17, 765-777.

Russell, B.R., Weiskittel, A.R., 2012. Assessing and modeling snag survival and decay dynamics for the primary species in the Acadian forest of Maine, USA. For. Ecol. Manag. 284, 230-240.

Saunders MR, Fraver S, Wagner RG (2011). Nutrient concentration of down woody debris in mixed wood forests in central Maine, USA. Silva Fennica 45: 197–210.

Sboarina, C., Cescatti, A., 2004. Il clima del Trentino – Distribuzione spaziale delle principali variabili climatiche. Report 33, Centro di Ecologia Alpina Monte Bondone, Trento, Italy.

Schmid, M.O., Gubler, S., Fiddes, J., Gruber, S., 2012. Inferring snowpack ripening and melt-out from distributed measurements of near-surface ground temperatures. The Cryosphere 6, 1127–1139.

Shorohova, E., Kapitsa, E., 2014. Influence of the substrate and ecosystem attributes on the decomposition rates of coarse woody debris in European boreal forests. For Ecol. Manag. 315, 173–184.

Shorohova, E., Kapitsa, E., Vanhna-Majamaa, I., 2008. Decomposition of stumps in a chronosequence after clear-felling vs. clear-felling with prescribed burning in a southern boreal forest in Finland. For. Ecol. Manag. 255, 3606–3612.

Skopp, J., Jawson, M.D., Doran, J.W., 1990. Steady-state aerobic microbial activity as a function of soil water content. Soil Sci. Soc. Am. J. 54, 1619–1625.

Stokland, J.N., Siitonen, J., Jonsson, B.G.. 2012. Biodiversity in dead wood. Cambridge, UK: Cambridge University Press.

Storaunet, K.O., Rolstad, J., 2002. Time since death and fall of Norway spruce logs in old-growth and selectively cut boreal forest. Can. J. For. Res. 32, 1801-1812.

Storaunet, K.O., 2004. Models to predict time since death of Picea abies snags. Scand. J. For. Res. 19, 250-260.

Strukelj, M., Brais, S., Quideau, S.A., Angers, V.A., Kebli, H., Drapeau, P., Oh, S.-W., 2013. Chemical transformations in downed logs and snags of mixed boreal species during decomposition. Can. J. For. Res. 43, 785-798.

Tarasov, M.E., Birdsey, R.A., 2001. Decay rate and potential storage of coarse woody debris in the

Leningrad Region. Ecol. Bull. 49, 137-147.

Tobin, B., Black, K., McGurdy, L., Nieuwenhuis, M., 2007. Estimates of decay rates of components of coarse wood debris thinned Sitka spruce forests. Forestry 80, 455-469.

Van der Wal, A., de Boer, W., Smant, W., van Veen, J.A., 2007. Initial decay of woody fragments in soil is influenced by size, vertical position, nitrogen availability and soil origin. Plant Soil 301, 189-201.

Van der Wal, A., Ottosson, E., de Boer, W., 2015. Neglected role of fungal community composition in explaining variation in wood decay rates. Ecology 96, 124-133.

Yatskov, M., Harmon, M.E., Krankina, O.N., 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Can. J. Forest Res. 33, 1211–1226.

Zhou, L., Dai, L., Gu, H., Zhong, L., 2007. Review on the decomposition and influence factors of coarse woody debris in forest ecosystem. Journ. For. Res. 18, 48–54.

Zielonka, T., 2006. When does dead wood turn into a substrate for spruce replacement? J. Veg. Sci. 17, 739–746.

Table 1
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Table 1. Characteristics of the study sites (Egli et al., 2006; Petrillo et al., 2016).

Plot ID	Elevation (m a.s.l.)	Aspect (°N)	Slope (°)	MAP[a] (mm y^{-1})	MAAT[a] (°C)	MAST[a] (°C)	Parent material	Dominating tree species	Land use	Soil classification (WRB)
North-facing sites										
N1	1180	340	31	950	5.6	7.3	Paragneiss debris	*Picea abies*	Natural forest (ecological forestry)	Chromi-Episkeletic Cambisol (Dystric)
N2	1390	0	28	1000	4.6	6.3	Paragneiss debris	*Picea abies*	Natural forest (ecological forestry)	Chromi-Episkeletic Cambisol (Dystric)
N3	1620	0	29	1060	3.5	5.8	Paragneiss debris	*Picea abies*	Natural forest (ecological forestry)	Chromi-Endoskeletic Cambisol (Dystric)
N4	1930	20	12	1180	1.4	5.0	Paragneiss debris, moraine material	*Larix decidua*	Originally used as pasture	Episkeletic Podzol
South-facing sites										
S6	1185	160	31	950	7.6–8.6[b]	8.1	Paragneiss debris	*Picea abies*	Ex-coppice, natural forest (ecological forestry)	Episkeleti-Endoleptic Cambisol (Chromi-Dystric)
S7	1400	145	33	1000	6.6–7.6[b]	8.7	Paragneiss debris	*Larix decidua*	Natural forest (ecological forestry)	Dystri-Endoskeletic Cambisol
S8	1660	210	33	1060	5.5–6.5[b]	6.0	Paragneiss debris	*Picea abies*	Natural forest (ecological forestry)	Skeletic Umbrisol
S9	1995	160	25	1180	3.4–4.4[b]	6.4	Paragneiss debris	*Larix decidua*	Ex pasture, natural forest	Skeletic Umbrisol

[a]MAAT = mean annual air temperature, MAP = mean annual precipitation (Sboarina and Cescatti, 2004); MAST = mean annual soil temperature (at 10 cm depth)
[b]thermal favourable conditions on south-facing sites included (according to Ascher et al., 2012)

Table 2
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Table 2. Regression functions tested for the temporal trends of the mass of deadwood and cellulose. Given are the R^2 values.

Site	Type of function Exponential function	Linear function	Polynomial function (2nd degree)	Exponential decay model (sigmoid function 1)	Logistic function (sigmoid function 2)
Deadwood					
N1	0.93	0.94	0.98	0.93	0.96
N2	0.28	0.26	0.29	0.27	0.25
N3	0.01	0.00	n.m.	0.00	0.00
N4	0.03	0.03	n.m.	0.03	0.01
S6	0.14	0.14	n.m.	0.16	0.11
S7	0.74	0.78	n.m.	0.52	0.33
S8	0.05	0.04	n.m.	0.04	0.07
S9	0.64	0.61	0.62	0.61	0.62
Cellulose					
N1	0.70	0.69	0.73	0.70	0.45
N2	0.72	0.69	0.69	0.69	0.60
N3	0.66	0.64	0.85	0.62	0.91
N4	0.50	0.53	n.m.	0.56	0.35
S6	0.28	0.30	n.m.	0.31	0.07
S7	0.50	0.50	n.m.	0.32	0.10
S8	0.24	0.25	n.m.	0.26	0.17
S9	0.76	0.75	0.80	0.69	0.92

n.m. not meaningful trends (decrease and later increase with time)

Table 3
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Table 3. Deadwood, cellulose and lignin decay constants k (y^{-1}) based on a) equation 1 (± standard error), b) the regression approach (exponential function). N = north-facing sites, S = south-facing sites.

Sites	N1	N2	N3	N4	Average N	S6	S7	S8	S9	Average S	Average all
Deadwood											
a)	0.080	0.036	-0.006	0.003	0.031	0.028	0.020	-0.009	0.145	0.046	0.039
	(0.060)	(0.051)	(0.025)*	(016)	(0.021)	(0.027)	(0.064)	(0.034)*	(0.065)	(0.028)	(0.017)
b)	0.071	0.057	0.003	0.021	0.038	0.043	0.021	0.002	0.101	0.042	0.040
Cellulose											
a)	0.072	0.096	0.131	0.103	0.101	0.042	0.011	0.029	0.393	0.119	0.110
	(0.043)	(0.067)	(0.036)	(0.062)	(0.024)	(0.045)	(0.042)	(0.032)	(0.080)	(0.052)	(0.028)
b)	0.078	0.128	0.135	0.127	0.117	0.062	0.077	0.052	0.347	0.116	0.117
Lignin											
a)	-0.004	0.035	0.030	-0.028	0.003	-0.018	-0.071	-0.047	0.130	-0.002	0.001
	(0.064)*	(0.029)	(0.057)	(0.059)*	(0.025)	(0.026)*	(0.060)*	(0.020)*	(0.005)	(0.028)*	(0.018)
b)	-0.004*	0.092	0.031	-0.007*	0.028	-0.027*	-0.024*	-0.029*	0.089	0.002	0.015

* negative values are not possible for a decay, but are due to measurement uncertainties.

Table 4. Some characteristic physico-chemical properties of the soils at the eight sites (values ± standard error)

Plot	Sand (%)	Silt (%)	Clay (%)	pH (H_2O)	Soil moisture (weight-%)
N01	59 (3)	26 (3)	15 (1)	5.27 (0.02)	30.8 (4.7)
N02	46 (7)	33 (5)	21 (3)	4.54 (0.20)	42.3 (3.6)
N03	51 (8)	31 (3)	18 (9)	4.39 (0.07)	47.9 (2.7)
N04	68 (4)	22 (2)	10 (3)	5.61 (0.07)	58.0 (3.8)
S06	56 (2)	30 (1)	14 (1)	5.76 (0.07)	33.9 (4.2)
S07	53 (6)	34 (6)	13 (0)	5.62 (0.04)	13.3 (1.3)
S08	60 (2)	21 (6)	19 (5)	5.46 (0.10)	34.0 (3.5)
S09	37 (5)	37 (4)	26 (1)	5.25 (0.05)	45.8 (5.1)

Table 5
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Table 5. Average correlation coefficients (±SD) obtained by data permutation (replicates) at each site. Decay rates and amount of cellulose (k(cell), Mass(cell)), lignin (Mass(lig)) and deadwood (k(deadwood), Mass(dw)) were related to the explanatory variables annual precipitation (MAP), mean annual soil temperature (MAST), MAAT (mean annual temperature), soil-pH, soil moisture (Moist) and clay content (clay).

	k(cell)		k(deadwood)		Mass(cell)		Mass(lig)		Mass(dw)	
	cor	corSD	cor	corSD	cor	corSD	cor	corSD	cor	corSD
All										
MAP	0.56*	0.17	0.07	0.28	-0.50*	0.20	-0.26	0.27	-0.40	0.26
MAST	-0.25	0.18	0.11	0.36	0.35	0.18	0.15	0.35	0.12	0.27
pH	-0.20	0.24	0.17	0.28	0.22	0.23	0.37	0.25	0.22	0.26
MAAT	-0.37	0.20	-0.03	0.24	0.40	0.20	0.16	0.32	0.21	0.31
Moist	0.41	0.13	0.12	0.26	-0.46	0.17	-0.24	0.35	-0.28	0.29
Clay	0.70*	0.12	0.24	0.35	-0.71*	0.13	-0.62*	0.21	-0.59*	0.20
North										
MAP	0.12	0.54	-0.32	0.53	-0.15	0.57	0.13	0.56	0.18	0.66
MAST	-0.11	0.52	0.39	0.55	0.09	0.56	-0.15	0.60	-0.11	0.63
pH	-0.23	0.52	0.04	0.43	0.18	0.48	0.47	0.49	0.15	0.60
MAAT	-0.18	0.58	0.37	0.47	0.07	0.56	-0.22	0.57	-0.24	0.65
Moist	0.00	0.55	-0.42	0.57	-0.23	0.54	0.21	0.57	0.11	0.63
Clay	0.11	0.49	-0.12	0.43	-0.14	0.52	-0.48	0.51	-0.18	0.58
South										
MAP	0.85*	0.11	0.49	0.43	-0.83*	0.14	-0.69*	0.13	-0.82*	0.10
MAST	-0.47	0.15	-0.15	0.50	0.46	0.19	0.39	0.31	0.40	0.17
pH	-0.78*	0.13	-0.42	0.42	0.77*	0.17	0.63*	0.15	0.76*	0.11
MAAT	-0.82*	0.12	-0.45	0.40	0.82*	0.14	0.68*	0.16	0.83*	0.09
Moist	0.71*	0.10	0.43	0.55	-0.73*	0.11	-0.74*	0.20	-0.62*	0.17
Clay	0.94*	0.06	0.54	0.46	-0.92*	0.06	-0.82*	0.11	-0.91*	0.05

* high ($R \geq 0.5$) and stable ($corSD \leq 0.20$) correlations

Table 6
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Table 6. Comparison of variables between south- and north-facing sites, and higher and lower sites (using the Mann-Whitney Test). Average/median values are given. Significant differences are indicated with * (p<0.05).

	North[1)]	South[1)]	Low[1)]	High[1)]	N1 – N3[1)]	S6 – S8[1)]
k_{cell}	0.101/0.095	0.119/0.034	0.055/0.029	0.164/0.095	0.100/0.096*	0.027/0.012*
$k_{deadwood}$	0.031/0.023	0.046/0.023	0.041/0.023	0.036/0.023	0.037/0.023	0.013/0.006
M_{cell}	8.29/8.28	8.32/9.36	9.061/9.45	7.54/8.28	8.29/8.19*	9.53/9.77*
M_{lign}	6.95/6.82	7.041/7.29	7.19/7.06	6.93/6.85	6.95/6.82	7.041/7.29
$M_{deadwood}$	21.35/21.23	21.55/22.74	22.07/21.75	20.28/21.92	21.14/21.20	23.03/23.23

[1)] k_{cell} (decay constant of cellulose), k_{lign} (decay constant of lignin), $k_{deadwood}$ (decay constant of deadwood), $M_{deadwood}$ (mass of deadwood), M_{cell} (mass of cellulose = concentration × dry weight of wood block), M_{lign} (Mass of lignin = concentration × dry weight of wood block), North (north-facing sites), South (South-facing sites), Low (sites < 1500 m asl), High (sites > 1500 m asl), N1 – N3 (north-facing sites except the highest site N4), S6 – S8 (south-facing sites except the highest site S9)

Table 7
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Table 7. Relative proportion (sum = 100%) of phyllosilicates (value, ±measurement error) in the clay fraction of the studied soils (according to Egli et al., 2006, 2007)

Plot	Elevation (m a.s.l.)	Smectite–Mica (%)	Smectite (%)	Chlorite (%)	HIV (%)	Vermiculite (%)	Mica (%)	Mica–HIV (%)	Kaolinite (%)
N1	1180	0	3±1	3±1	17±3	7±2	40±6	26±4	5±2
N2	1390	0	25±4	6±2	8±2	22±3	11±2	21±3	7±2
N3	1620	10±2	30±5	0	0	44±7	14±3	0	2±1
N4	1930	0	9±2	4±2	9±2	4±2	41±6	24±4	10±2
S6	1185	0	0	2±1	6±2	1±1	67±9	17±3	7±2
S7	1400	0	0	4±2	10±2	9±2	27±4	41±6	9±2
S8	1660	0	0	6±2	13±2	32±5	15±3	28±5	5±2
S9	1995	0	3±1	2±1	6±2	23±3	22±3	35±5	10±2

HIV = Hydroxy-interlayered vermiculite, Smectite–Mica = interstratified smectite/mica, Mica-HIV = interstratified mica/HIV

Figure captions

Fig. 1. Location of the investigation area in Trentino (Italy).

Fig. 2. Set-up of the experimental plots with wood blocks. For each time segment, three replicates were used. Wood blocks with a uniform shape and size were placed into the 'mesocosms' (i.e. open tubes inserted into the soil) on the soil surface and left for the indicated duration (weeks).

Fig. 3. Weight (± standard error) of the wood blocks (placed into mesocosms) as a function of time (0 – 2 years), site (altitude) and exposure (north vs south).

Fig. 4. Amount of cellulose (= concentration × dry weight of wood block; weight ± standard error) as a function of time (0 – 2 years), site (altitude) and exposure (north vs south).

Fig. 5. Amount of lignin (= concentration × dry weight of wood block; weight ± standard error) in the wood blocks as a function of time (0 – 2 years), site (altitude) and exposure (north vs south).

Fig. 6. Comparison of exponential, linear, sigmoid (2 types; sigmoid function 1 (eq. 4) and sigmoid function 2 (eq. 5)) and polynomial (2^{nd} order) best-fit decay model for deadwood (dry weight of wood blocks) and amount of cellulose (concentration × dry weight of wood block) for site S9.

Fig. 7. Comparison between decay constants of cellulose (k1, [y^{-1}]) and deadwood (k2, [y^{-1}]) and explanatory variables such as the clay content [%], mean annual temperature MAP [mm y^{-1}], mean annual soil temperature MAST [°C], soil-pH, mean annual temperature MAAT [°C] and soil moisture [%]. The different colours refer to the individual sites.

Fig. 8. Comparison between the mass of cellulose [g], lignin [g] and deadwood [g] at the end of the decay experiment with explanatory variables such as the clay content [%], mean annual temperature MAP [mm y^{-1}], mean annual soil temperature MAST [°C], soil-pH, mean annual temperature MAAT [°C] and soil moisture [%]. The different colours refer to the individual sites.

Figure 1
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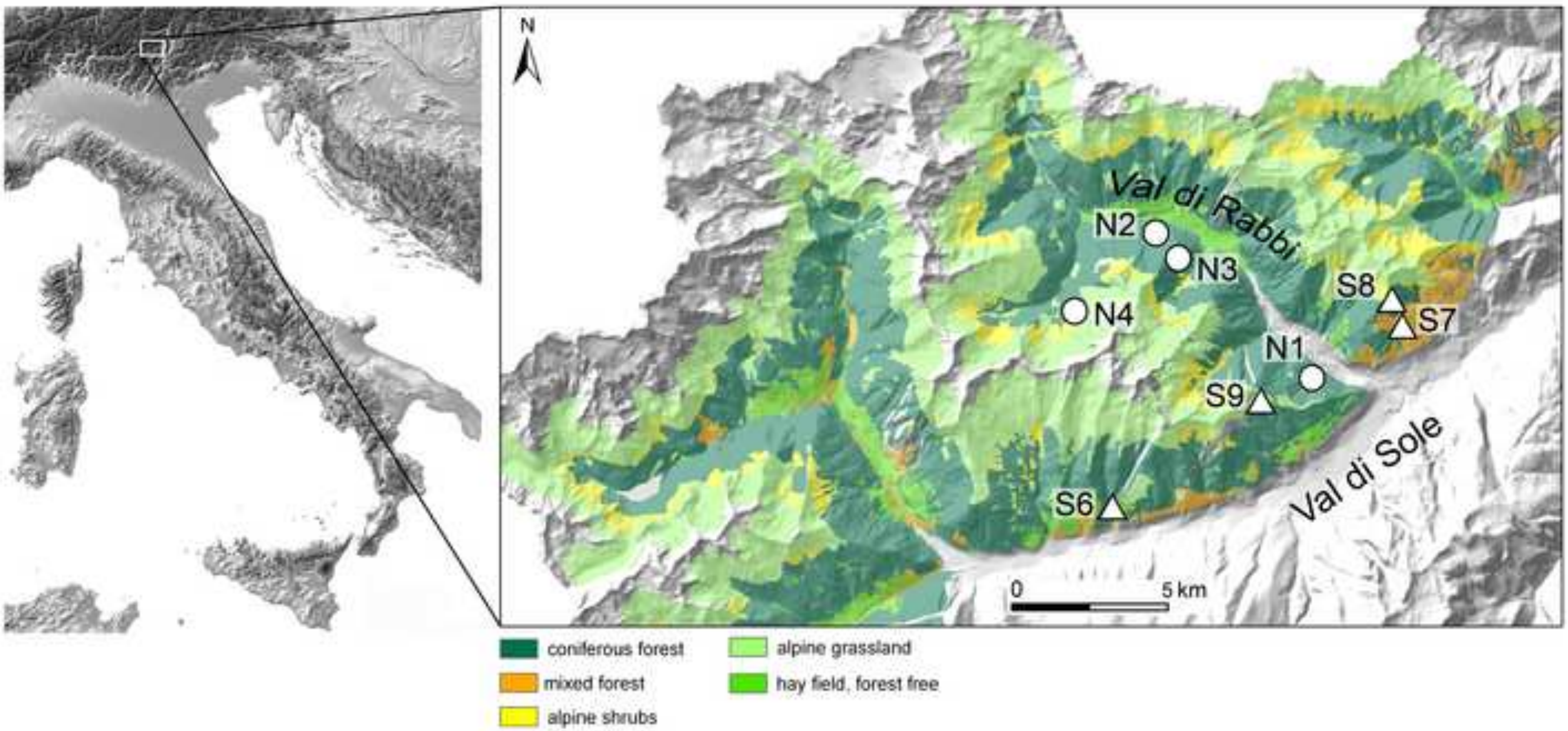

Figure 2
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Figure 3

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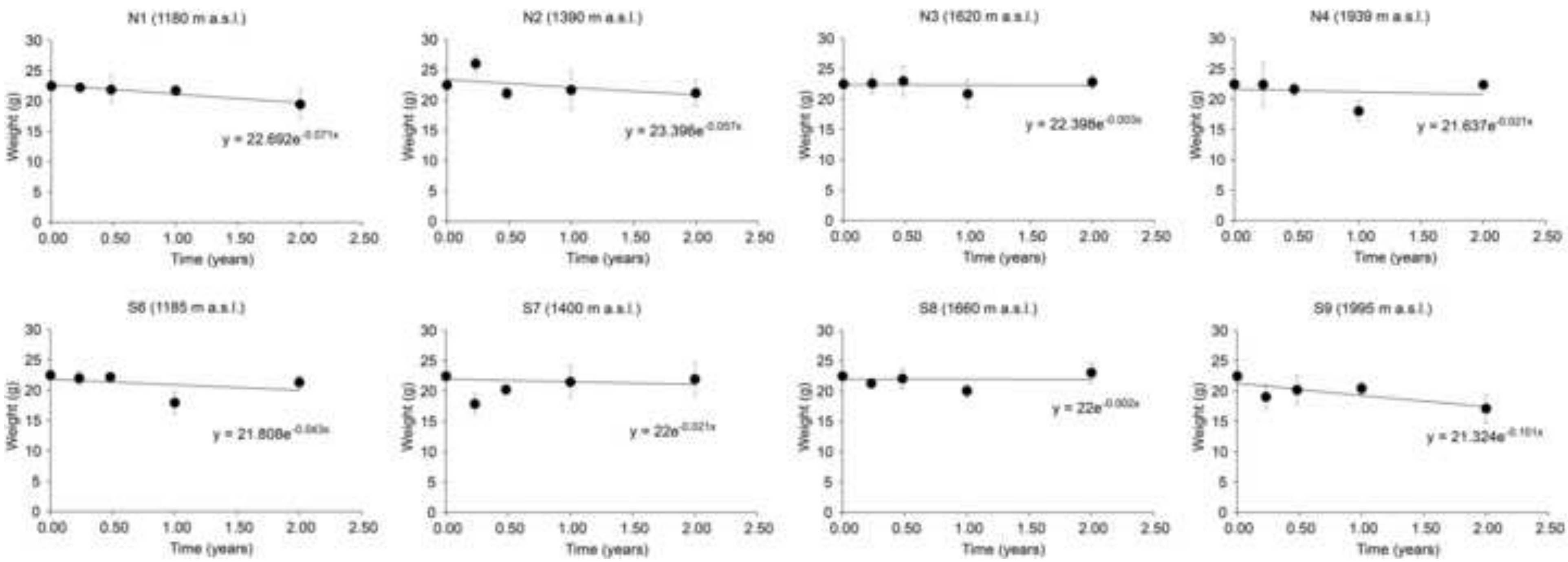

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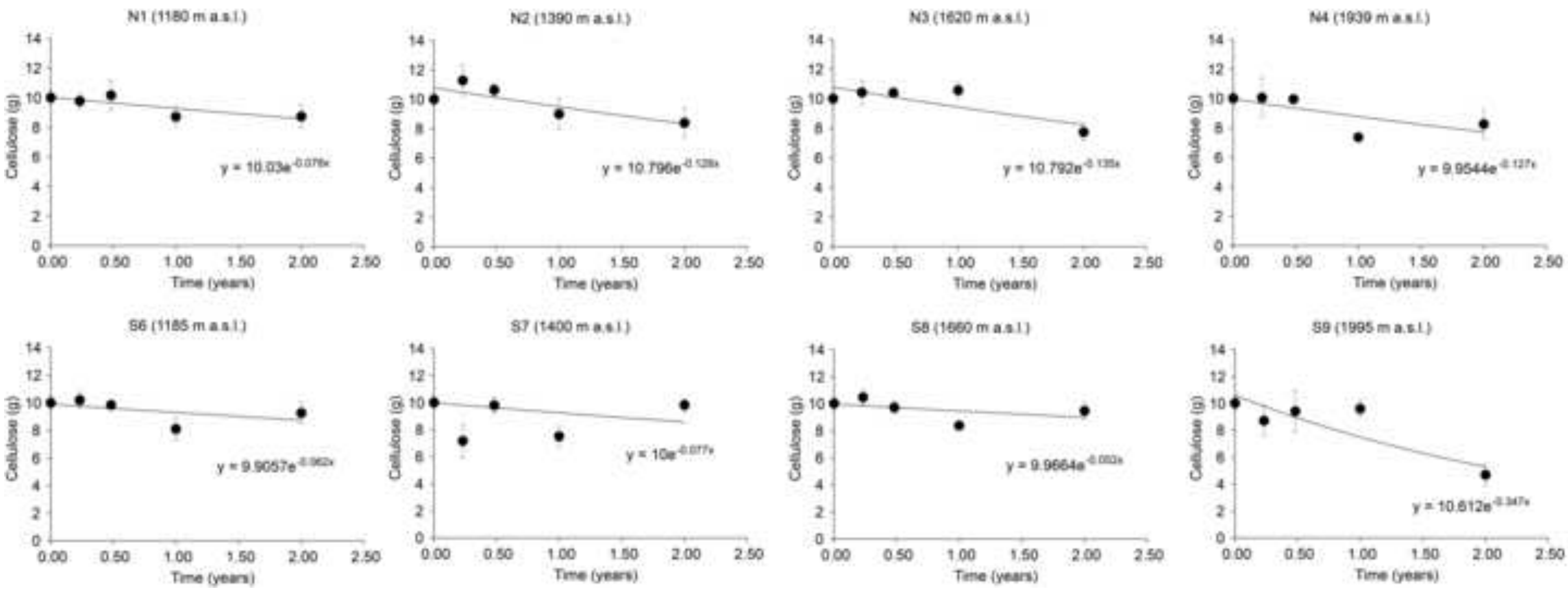

Figure 5

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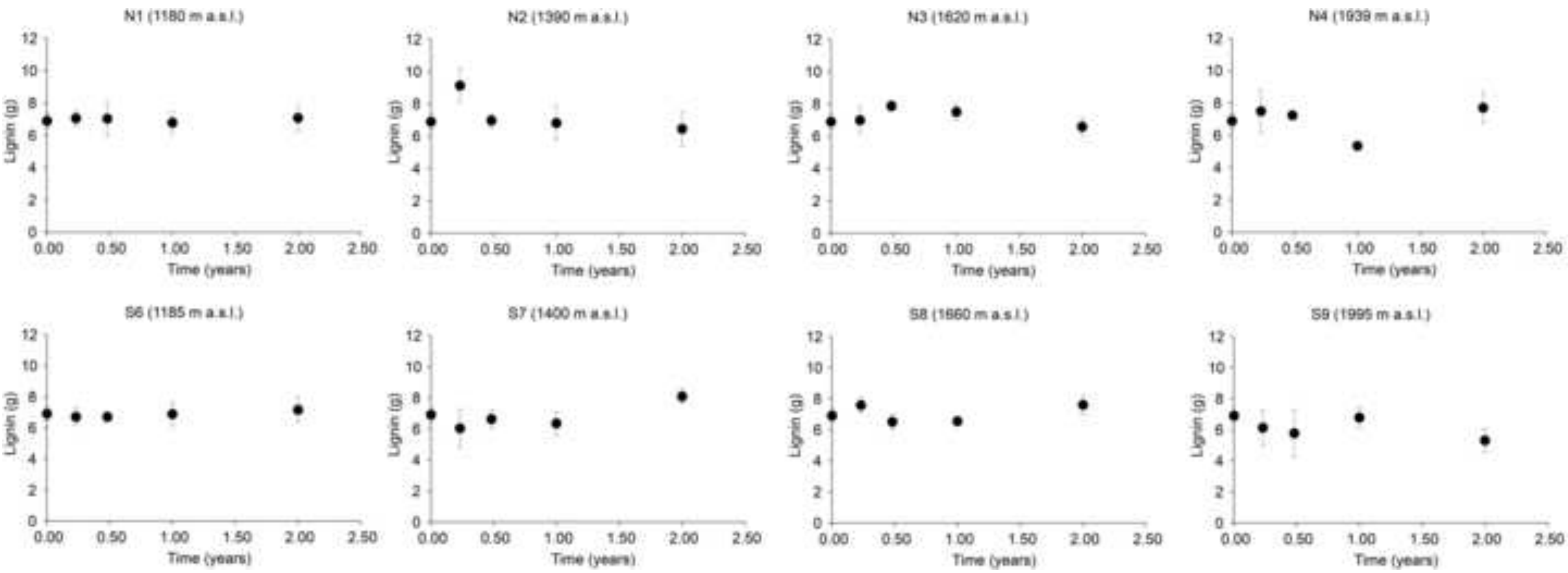

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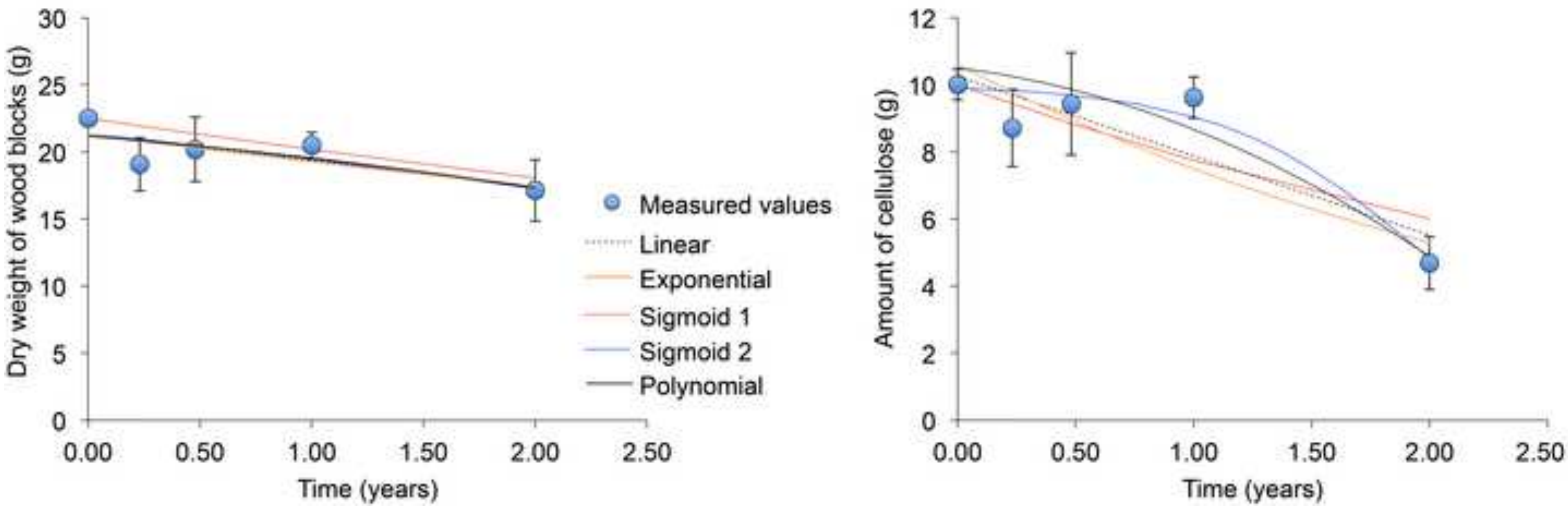

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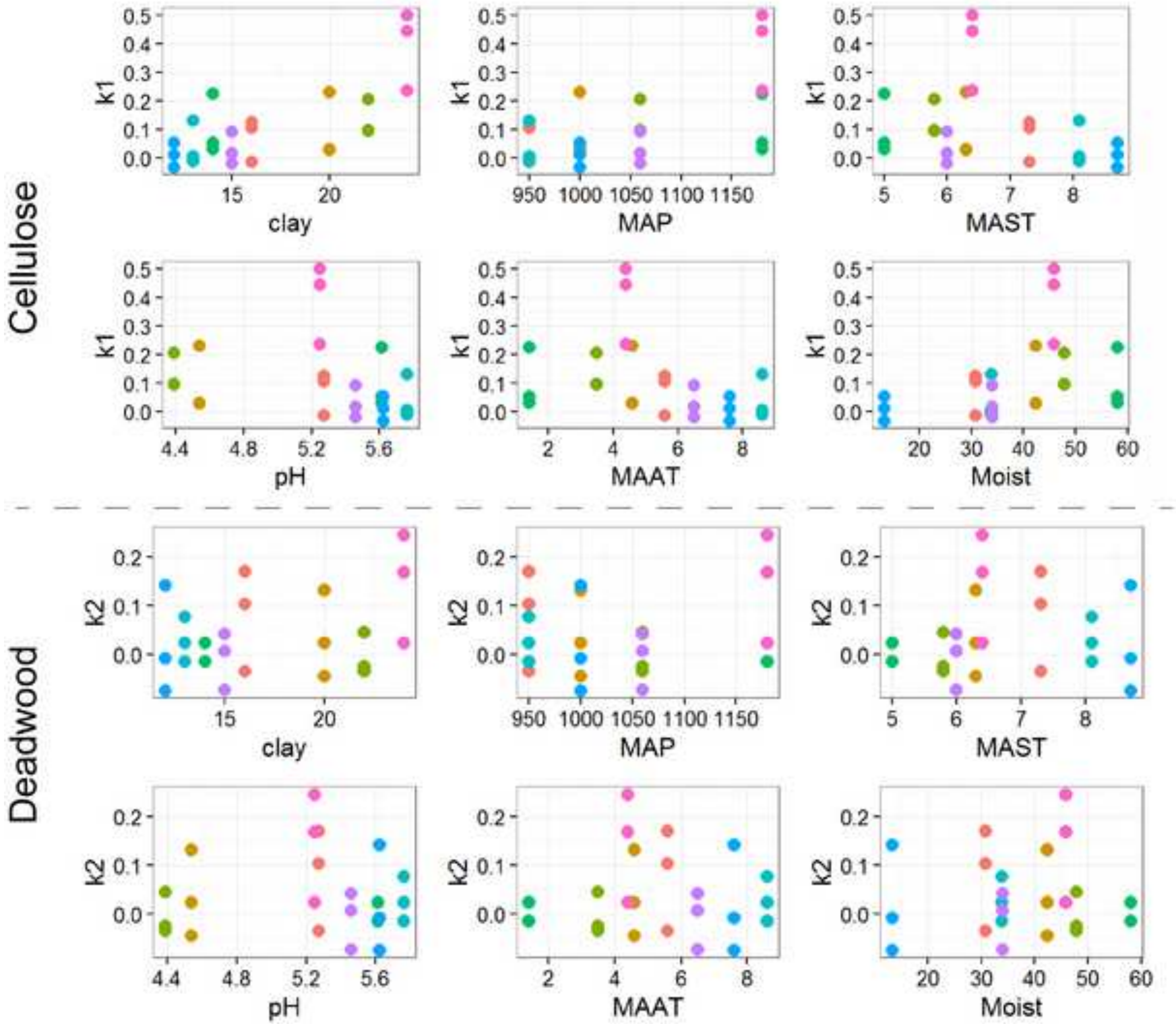

Figure 8

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